

Nitrogen Fertilization Affects Bahiagrass Responses to Elevated Atmospheric Carbon Dioxide

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ABSTRACT

Increased atmospheric CO₂ and temperature typically lead to greater DM (dry matter) production of grassland plants; however, limited plant N may reduce this response. A 2-yr study (1998–1999) was conducted to evaluate the effects and interactions among atmospheric CO₂, temperature, and N fertilization rate on yield and nutritive value of 'Pensacola' bahiagrass (*Paspalum notatum* Flüggé). Bahiagrass was field grown in Millhopper fine sand (loamy, siliceous Grossarenic Paleudult) under greenhouses with controlled atmospheric CO₂ and temperature. Atmospheric CO₂ levels were 360 and 700 µmol mol⁻¹, and temperatures were B (baseline, corresponding to ambient in the greenhouse), B + 1.5°C, B + 3.0°C, and B + 4.5°C. Bahiagrass was fertilized at 80 kg N ha⁻¹ (BG-80) or 320 kg N ha⁻¹ (BG-320). Dry matter yield for BG-80 remained the same regardless of CO₂ level (7.5 and 6.3 Mg ha⁻¹ in Years 1 and 2), but BG-320 DM yield increased with increasing CO₂ concentration in three of four harvests in Year 1 and from 14.8 to 17.3 Mg ha⁻¹ in Year 2. Total N harvested response followed a similar trend as DM yield. Increasing temperature from B to B + 4.5°C had a positive effect on DM yield of BG-80 (23%) and a lesser positive effect on BG-320 (9% increase). Bahiagrass nutritive value increased due to greater N fertilization, but elevated CO₂ concentration and temperature had no effect. Nitrogen fertilization affected bahiagrass DM yield response to CO₂, but not the nutritive value response to elevated atmospheric CO₂ or temperature.

CLIMATE CHANGE, or the increase in atmospheric CO₂ and associated global warming, has fueled studies of plant response to CO₂ and temperature. There is widespread evidence that elevated CO₂ increases plant growth (Kimball, 1983; Morgan et al., 2001; Newman et al., 2001), but the effects of increasing temperature on biomass yield generally have not been as pronounced as those of CO₂ (Cure and Acock, 1986; Fritschi et al., 1999). Greater increases in growth under elevated CO₂ are expected for plants of the C₃ carbon fixation pathway (30–40%, Kimball, 1983) than for C₄ species (10%, Newton, 1991).

Most grassland ecosystems are N limited, resulting in reduced productivity and contributing to lower herbage nutritive value (Wedin, 2004). The relationship of grass

N status and response to increasing atmospheric CO₂ and temperature is of interest because reduced nutrient availability could potentially limit plant responses to environmental changes that normally stimulate growth (Jones, 1997). The C₄ bahiagrass, with leaf N concentration of <10 g kg⁻¹, showed only a trend toward increasing yield with increasing atmospheric CO₂ (Newman et al., 2001). It is uncertain whether the limited response to CO₂ simply was typical for a C₄ grass, or if the lack of response to CO₂ was due in part to N deficiency. In the same study, the C₃ legume rhizoma peanut (*Arachis glabrata* Benth.) increased yield 25% as CO₂ increased from 360 to 700 µmol mol⁻¹. It is not clear to what extent this greater yield response of the legume than the grass to elevated CO₂ was due to the C₃ pathway of the legume and to what extent it was due to greater N concentration of the legume relative to bahiagrass. Other studies, however, have shown greater response of legumes than C₃ grasses to elevated CO₂ in N-limiting soils (Hebeisen et al., 1997), suggesting that plant N status plays a critical role in CO₂ response.

More information is needed to determine if C₄ grass DM production and nutritive value response to climate change factors interact with N fertilization rate. The hypothesis for the current study was that bahiagrass yield response to elevated CO₂ concentration is greater under high than under low N fertilization. The specific objectives were to quantify the effects of N fertilization rate on bahiagrass yield and nutritive value responses to increasing temperature and atmospheric CO₂ concentration.

MATERIALS AND METHODS

This experiment was conducted during 1998 and 1999 at the Irrigation Research and Education Park, University of Florida, Gainesville (29°38' N, 82°22' W) and was part of a long-term study (Boote et al., 1999) of bahiagrass and rhizoma peanut growth in TGGs (temperature gradient greenhouses). Four TGGs (27 m long by 4.4 m wide) were constructed over field soils. A detailed description of the construction and design is given in Sinclair et al. (1995) and Fritschi et al. (1999). Lengthwise, half of each TGG was planted to bahiagrass and the other half to rhizoma peanut, separated by a 0.7-m center alley. Stands were planted in 1995 in undisturbed natural Millhopper fine sand at a rate of 30 kg ha⁻¹ seed (bahiagrass) and 1.6 Mg ha⁻¹ fresh weight of rhizomes (rhizoma peanut). Soil pH was 6.2 to 6.7, and soil organic matter ranged from 12 to 15 g kg⁻¹. Mehlich I extractable P, K, and Mg at the site were 79 to 97, 6 to 11, and 98 to 115 mg kg⁻¹, respectively.

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Abbreviations: B, baseline temperature; BG-80, bahiagrass fertilized at 80 kg N ha⁻¹ yr⁻¹; BG-320, bahiagrass fertilized at 320 kg N ha⁻¹ yr⁻¹; DM, dry matter; IVDOM, in vitro digestible organic matter; TGG, temperature gradient greenhouse.

For this study, the N rates were imposed only on 'Pensacola' bahiagrass and only bahiagrass data will be reported. Treatments were a factorial arrangement of two CO₂ levels (360 and 700 $\mu\text{mol mol}^{-1}$, with two TGGs per level of CO₂), four temperatures (B, B + 1.5°C, B + 3.0°C, and B + 4.5°C, created in strips across the width of each greenhouse), and two levels of N fertilizer (80 and 320 kg N ha⁻¹, randomly split within each temperature strip of bahiagrass; Fig. 1). Plot size was 5 m² (2.5 by 2 m).

Temperature and CO₂ treatments were continuously imposed in TGGs year-round. Carbon dioxide was injected in two of the four TGGs, using a distribution system located at the inlet end of the TGG, and regulated through an algorithm

using inputs from ventilation fan speed inside the TGG, current measurements, and feedback of recent past values of atmospheric CO₂ concentrations. The four temperature zones were created in a gradient at 5.5-m increments, along their length, from the inlet to the outlet end of the TGGs. Solar radiation reaching the TGGs was the primary heat source during the day. Temperature gradients were produced by regulating the rate of unidirectional ventilation relative to heat input from incident solar radiation. At night and during low solar irradiance periods, hot air (120°C) was infused at the beginning of the three 5.5-m elevated-temperature zones. Each zone was represented by temperature measurements recorded at 0.6 m above soil surface. A controller and data logger system based on readings from aerial thermocouples placed at 0.9 m above ground level over plots adjacent to inlet and outlet sections was used to adjust the exhaust fan speed (increased or decreased) to maintain the target temperature difference (4.5°C) between inlet and outlet ends of the TGGs.

The desired temperature gradient was achieved in each of the TGGs as illustrated for 1998 (Fig. 2). Detailed descriptions of establishment procedures in 1995, maintenance of the forages from 1995 to 1998, setting and controlling of artificial temperature gradient and environmental conditions, and experimental procedures for that period have been described (Fritsch et al., 1999; Newman et al., 2001). Refer to these sources for additional information.

Fertilization and Irrigation

Bahiagrass is a rhizomatous warm-season perennial forage that starts growth in March of most years in North Florida. Fertilizer was split applied starting in March and continuing until shortly before the last harvest of each year. Total annual applications to all plots were 36 kg P and 152 kg K ha⁻¹. Annual N applications were according to treatment. For each plot, the annual total of all nutrients was divided into 16 equal applications; there were four applications during the growth period leading up to each of the four harvests per year. Thus each application for BG-80 included 5 kg N ha⁻¹ and for BG-320 included 20 kg N ha⁻¹.

Each TGG was equipped with a double-overlapping micro-jet sprinkler irrigation system designed to apply 7 to 8 mm d⁻¹ during the 8- to 9-mo growing season. During November through February, the irrigation amount was reduced to 3 to 4 mm d⁻¹.

Weed and Pest Control

Plots were hand weeded as needed. During winter, the major weed was narrow leaf cudweed (*Gnaphalium falcatum*

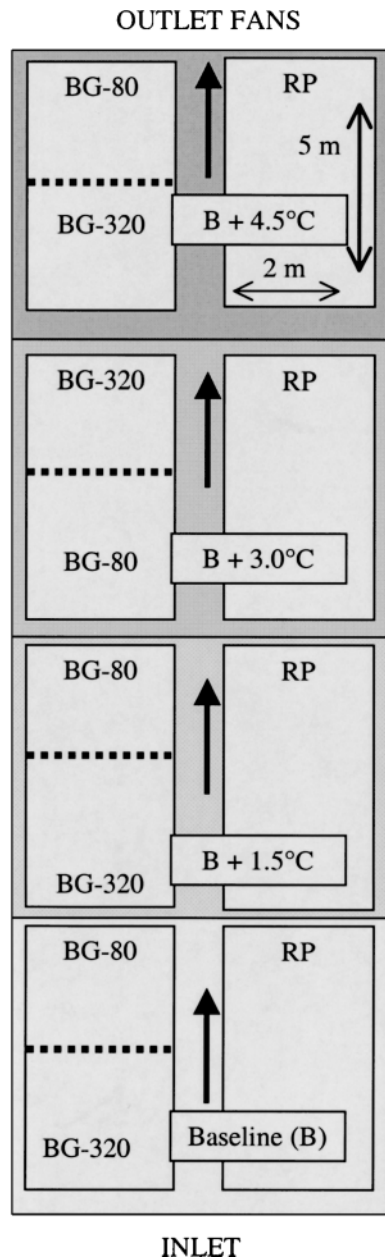


Fig. 1. Example of treatment layout in a temperature-gradient greenhouse (not to scale). One greenhouse is shown and represents one replicate of one CO₂ main plot. Unidirectional arrows indicate the direction of airflow. BG-80 and BG-320 are bahiagrass fertilized at 80 and 320 kg N ha⁻¹ yr⁻¹, respectively; RP = rhizomatous peanut stands on which data were not collected for this study.

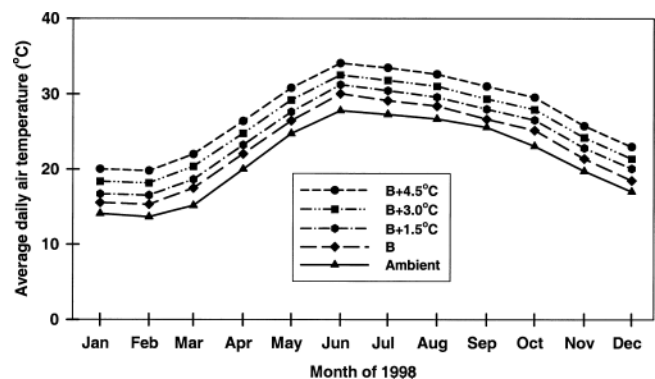


Fig. 2. Monthly averages of average daily temperature in Greenhouse 1 for baseline (B) through B + 4.5°C temperature treatments during 1998.

Lam) of the Compositae family; during summer it was long-stalked phyllanthus (*Phyllanthus tenellus* Roxb.) of the Euphorbiaceae family, a C₄ plant. Phyllanthus was very prolific at the warmest temperatures and enriched CO₂.

The major pest of bahiagrass was mole cricket (*Scapteriscus borelli* Giglio-Tos). Labeled sprays and baits were applied on an as-needed basis for control.

Plant Sampling and Nutritive Value Analysis

Plots were harvested on 18 May, 6 July, 24 Aug., and 9 Nov. 1998; and 27 May, 8 July, 30 Aug., and 16 Nov. 1999. These dates correspond with Day of the Year 138, 187, 236, and 313 in 1998; and Day of the Year 147, 189, 232, and 310 in 1999. Herbage mass was measured by clipping two randomly placed 0.25-m² quadrats per plot to a 5-cm stubble, compositing herbage from the two quadrats within a plot, and drying the herbage for 48 h at 55°C. An additional sample of approximately 400 g fresh weight was clipped to a 5-cm stubble from each plot to assess nutritive value. Samples for nutritive value were oven dried for 48 h at 55°C and ground to pass through a 1-mm mesh screen in a Wiley mill. Ground forage samples were analyzed for DM, IVDOM (in vitro digestible organic matter), and total N concentration. A 1-g aliquot was used for determining absolute DM (drying at 105°C for 15 h; AOAC International, 1990). Total organic matter was determined by ashing for 15 h at 550°C (AOAC International, 1990). The two-stage technique of Moore and Mott (1974) was used to determine IVDOM. Total N was determined using a micro-Kjeldahl method, a modification of the aluminum block digestion technique described by Gallaher et al. (1975). Crude protein was calculated as N × 6.25 (AOAC International, 1990).

Data Analyses

Data were analyzed using mixed-model methods (SAS Institute, 1996). In all models, effects of CO₂ concentration, temperature, N rate, year, and their interactions, were considered fixed effects. Greenhouses nested within CO₂ levels were modeled as random effects. There were several treatment × year interactions; thus, data are presented by year. Orthogonal polynomial contrasts (linear, quadratic, and cubic) were used to determine the nature of responses to temperature. All means reported in the text are least squares means. Treatments were considered different if $P \leq 0.10$.

RESULTS AND DISCUSSION

Total Dry Matter Yield and Nitrogen Harvested

Nitrogen × Carbon Dioxide Interaction Effects

Probability values are presented in Table 1 for the effects of year, N rate, CO₂, temperature, and their interactions on DM yield and N harvested. There was a CO₂ × N rate × year interaction for total annual DM yield and N harvested ($P < 0.01$ and $P = 0.09$, respectively), therefore data were analyzed by year. When analyzed by year, there was a CO₂ × N rate interaction ($P < 0.01$) for total DM yield in 1999 and a trend ($P = 0.22$) toward interaction in 1998 (Table 2).

The CO₂ × N rate interaction effect on DM yield (Table 2) occurred because total seasonal DM yield increased or tended to increase under enriched CO₂ conditions only for BG-320, while for BG-80 there was no response to elevated CO₂. In 1999, yield for BG-320

Table 1. Levels of probability (P) for the effects of year, CO₂, N rate, temperature (Temp), and their interactions on total dry matter (DM) harvested, N harvested, crude protein (CP), and in vitro digestible organic matter (IVDOM).

Source of variation	DM harvested	N harvested	CP	IVDOM
Year	0.16	<0.01	<0.01	<0.01
N rate	<0.01	<0.01	<0.01	<0.01
CO ₂	0.06	0.19	0.84	0.69
Temp	<0.01	0.05	0.66	0.48
N rate × year	<0.01	<0.01	0.14	0.14
CO ₂ × year	0.90	0.70	0.33	0.89
N rate × CO ₂	<0.01	<0.01	0.56	0.92
Temp × CO ₂	<0.01	0.11	0.76	0.65
Temp × year	0.86	0.86	0.91	0.56
N rate × temp	0.27	0.38	0.59	0.47
N rate × CO ₂ × year	<0.01	0.09	0.56	0.85
N rate × temp × year	0.24	0.40	0.79	0.59
N rate × temp × CO ₂ × year	0.11	0.60	0.43	0.99

was greater at elevated CO₂ than at ambient, and in 1998 there was a trend ($P = 0.12$) toward greater yield at higher atmospheric CO₂ concentration. Presence of only a trend for the total-season response in 1998 can be attributed to the first harvest, at which there was no effect of CO₂ level on yield of BG-320 plots (Fig. 3). In three subsequent harvests that year, yield was greater for elevated than ambient CO₂. Absence of a first-harvest CO₂ effect probably reflected the low-N status of the BG-320 plots at initiation of the experiment, a hypothesis that is supported by markedly lower Harvest 1 (18 May) yields (2.7 Mg ha⁻¹) in 1998 compared with any subsequent harvest (~4.0 Mg ha⁻¹) in 1998 or 1999 (Fig. 3). During the 2 yr preceding the current research, the BG-320 plots had received 80 kg N ha⁻¹ yr⁻¹ and yield decreased from year to year. In addition, herbage N concentration during those 2 yr was <10 g kg⁻¹ (Newman et al., 2001).

The magnitude of the yield difference between elevated and ambient CO₂ for BG-320 plots was consistent for the final two harvests of 1998 and all harvests in 1999 (Fig. 3), although somewhat greater standard errors made it impossible to detect differences between CO₂ levels in two harvests of 1999. For BG-80, DM yields were not affected by atmospheric CO₂ concentration, and they averaged 7.5 and 6.3 Mg ha⁻¹ yr⁻¹ in 1998 and 1999, respectively. In addition, there was no effect of

Table 2. Nitrogen rate × CO₂ interaction means for total annual dry matter harvested. Data are means averaged across four temperatures and two replicates ($n = 8$).

Treatment†	1998			1999		
	CO ₂ , μmol mol ⁻¹		P‡	CO ₂ , μmol mol ⁻¹		P‡
	360	700		360	700	
	–Mg ha ⁻¹ yr ⁻¹ –			–Mg ha ⁻¹ yr ⁻¹ –		
BG-80	7.1	7.8	0.37	6.6	6.0	0.29
BG-320	15.0	16.1	0.12	14.8	17.3	0.02
P§	<0.01	<0.01		<0.01	<0.01	
SE	0.44			0.37		

† Bahiagrass fertilized with either 80 (BG-80) or 320 kg N ha⁻¹ yr⁻¹ (BG-320).

‡ Probability value for CO₂ effect within year and N rate.

§ Probability value for N rate effect within year and CO₂ level.

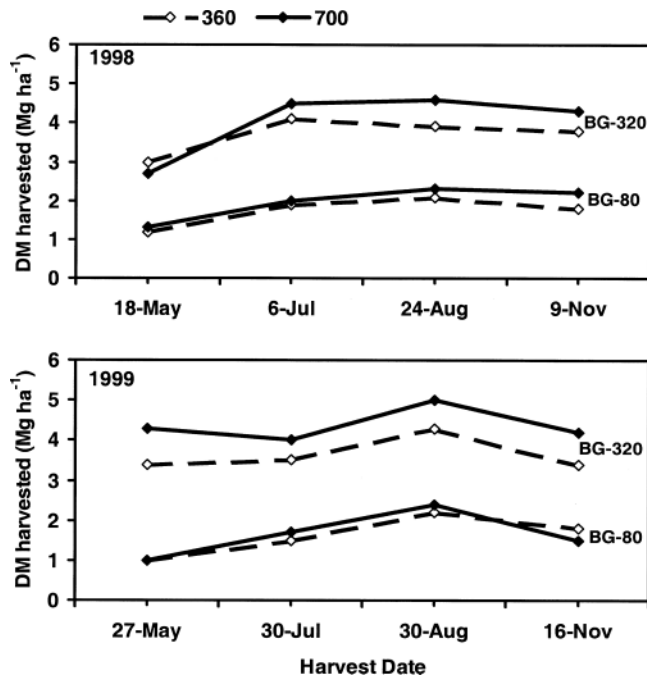


Fig. 3. Dry matter (DM) yield by harvest of bahiagrass fertilized at 80 (BG-80) or 320 kg N ha⁻¹ yr⁻¹ (BG-320) under ambient (360 μmol mol⁻¹) and enriched (700 μmol mol⁻¹) CO₂ levels for 1998 and 1999. There were no CO₂ effects at any harvest for BG-80 in 1998 ($P > 0.16$) or 1999 ($P > 0.50$). For BG-320, P values for Harvests 1 through 4 were 0.26, 0.02, 0.09 and 0.05, respectively, in 1998, and 0.09, <0.01, 0.42, and 0.18, respectively, in 1999.

CO₂ on DM yield for BG-80 at any of the eight harvest dates (Fig. 3).

Nitrogen deficiency has been thought to limit yield of grasses under enriched atmospheric CO₂ conditions (Wong, 1979; Grant et al., 2001). Similarly, greater N fertilization has been associated with greater herbage accumulation responses to CO₂ enrichment in C₄ grasses (Ghannoum and Conroy, 1998), but this response has not been totally consistent. Lack of response to CO₂ by N-fertilized treatments was attributed to a CO₂-induced greater N demand (Morgan, 2000), to reduced N remobilization to shoot regrowth (Skinner et al., 1999), and in other cases, the lack of response was associated with differences in above- and belowground DM partitioning (Morgan et al., 2001) or with allocation of the additional N to the root system for exploitation of a larger soil volume (Hebeisen et al., 1997). Data from the current study support the conclusions that responsiveness to a CO₂-enriched environment may be mediated by the N status of the plant (Greenwood et al., 1990; Stitt and Krapp, 1999), and N deficiency may not allow the expected yield response to elevated CO₂ (Zanetti et al., 1997).

Total seasonal DM yields were greater for the high than low N rate in both years and at both levels of CO₂ (Table 2), with BG-320 annual yields two to almost three times greater than BG-80. This magnitude of bahiagrass response to N has been observed by others (Burton et al., 1997; Twidwell et al., 1998), despite the reputation of bahiagrass as being adapted to low-input systems (Gates et al., 2004).

Table 3. Nitrogen rate × CO₂ interaction effect for total annual N harvested. Data are means averaged across four temperatures and two replicates ($n = 8$).

Treatment†	1998			1999		
	CO ₂ , μmol mol ⁻¹			CO ₂ , μmol mol ⁻¹		
	360	700	P‡	360	700	P‡
	— kg ha ⁻¹ yr ⁻¹ —			— kg ha ⁻¹ yr ⁻¹ —		
BG-80	63	66	0.81	66	59	0.39
BG-320	179	194	0.32	197	225	0.02
P§	<0.01	<0.01		<0.01	<0.01	
SE	8			5		

† Bahiagrass fertilized with either 80 (BG-80) or 320 kg N ha⁻¹ yr⁻¹ (BG-320).

‡ Probability value for CO₂ effect within year and N rate.

§ Probability value for N rate effect within year and CO₂ level.

Total N harvested (Table 3) followed a similar pattern to that of total DM harvested. The CO₂ × N rate interaction for total N harvested approached significance in 1998 ($P = 0.20$) and was significant in 1999 ($P < 0.01$). Total annual N harvested did not respond to enriched CO₂ conditions at BG-80 in either year, and across CO₂ levels averaged 64.5 and 62.5 kg ha⁻¹ yr⁻¹ in 1998 and 1999, respectively. For BG-320, total N harvested increased from 192 to 224 kg ha⁻¹ yr⁻¹ with increasing CO₂ concentration. Total N harvested was greater for BG-320 than BG-80 in both years and at both levels of CO₂ (Table 3).

Temperature Effects

There was a temperature × CO₂ interaction (Table 4, $P < 0.01$) for total annual DM yield. Interaction occurred because the response to temperature at ambient CO₂ was greater than at elevated CO₂ concentration. At ambient CO₂, total DM harvested increased from 9.9 Mg ha⁻¹ yr⁻¹ at B to 12.2 Mg ha⁻¹ yr⁻¹ at B + 4.5°C (linear and cubic effects, $P < 0.01$). This is a 23% increase, compared with only a 9% increase for total DM harvested at the enriched CO₂ concentration. The lesser response at elevated CO₂ levels suggests that there may be some acclimation to greater temperatures in the CO₂-enriched environment (Sage and Kubien, 2003). Dry matter harvested at elevated CO₂ increased from B (11.0 Mg ha⁻¹) to B + 1.5°C (12.4 Mg ha⁻¹), but did not change significantly thereafter.

Table 4. Carbon dioxide × temperature interaction means for total annual DM harvested. Data are means across two N rates, 2 yr, and two replicates ($n = 8$).

Temperature	CO ₂ , μmol mol ⁻¹		<i>P</i> ‡
	360	700	
	—Mg ha ⁻¹ yr ⁻¹ —		
B‡	9.9	11.0	0.03
B + 1.5°C	11.1	12.4	0.01
B + 3.0°C	10.1	12.2	<0.01
B + 4.5°C	12.2	12.0	0.24
SE	0.3	0.3	
Contrast§	L, C	Q	
<i>P</i>	<0.001, 0.001	0.008	

† Probability value for CO₂ effect within temperature.

‡ Baseline temperature, defined as ambient temperature in the greenhouse.

§ Orthogonal polynomial contrast of temperature effect within CO₂ treatment. L = linear, Q = quadratic, C = cubic.

Table 5. Year and N-rate means for herbage in vitro digestible organic matter (IVDOM) and crude protein (CP) concentrations. Data are means across four temperatures and two replicates ($n = 8$). There was no N rate \times year interaction for IVDOM ($P = 0.14$) or CP ($P = 0.14$).

Treatment	IVDOM			CP		
	1998	1999	Mean	1998	1999	Mean
	g kg ⁻¹			g kg ⁻¹		
BG-80	443	422	432 b†	54	63	58 b
BG-320	487	455	471 a	76	83	79 a
Mean	465 a‡	438 b		64 b	73 a	
SE			7			2

† N rate means across years not followed by the same letter are different ($P < 0.01$).

‡ Year means within a response variable not followed by the same letter are different ($P < 0.01$).

For total annual N harvested, there were temperature effects but no temperature \times CO₂ interaction. Total N harvested increased with increasing temperature from 126 kg ha⁻¹ yr⁻¹ at B to 139 kg ha⁻¹ yr⁻¹ at B + 4.5°C (linear effect, $P = 0.07$). The overall increase in N harvested across the range of increasing temperature was 10%.

Nutritive Value

Probability values are presented in Table 1 for the effects of year, N rate, CO₂, temperature, and their interactions on IVDOM and crude protein. Bahiagrass IVDOM and crude protein were affected only by year and N rate. In vitro organic matter digestibility was consistently greater for BG-320 than BG-80 in both years (Table 5). Crude protein followed the same trend as IVDOM and, overall, the N-rate effect was greater on crude protein than on IVDOM.

The crude protein response to N rate is well established in the literature, while the positive effect on IVDOM is less consistent. There are, however, several recent studies with limpograss [*Hemarthria altissima* (Poir.) Stapf & Hubb; da Lima et al., 1999], stargrass (*Cynodon nlemfuensis* Vanderyst; Hernández Garay et al., 2004), and bahiagrass (Stewart et al., 2003) that show a positive response of herbage IVDOM to increasing N rates. Other studies have shown decreasing nutritive value of several warm-season forages to increasing temperature, including rhizoma peanut (Newman et al., 2005), 'Coastal' and common bermudagrass [*Cynodon dactylon* (L.) Pers.], bahiagrass, and dallisgrass (*P. dilatatum* Poir.; Henderson and Robinson, 1982). The nutritive value response to CO₂ has been inconsistent and generally small (Seligman and Sinclair, 1995).

CONCLUSIONS

The results of this study support the conclusion that low bahiagrass N status may limit the response of this C₄ species to elevated CO₂. The yield response of well-fertilized bahiagrass to CO₂ enrichment was from 7 to 17%, within the range expected for C₄ plants, while bahiagrass that received inadequate N did not respond to elevated CO₂. This result implies that to make ef-

fective use of a potentially greater supply of C provided by elevated atmospheric CO₂ concentrations, plants growing in marginal soil-N environments probably will require additional N fertilizer.

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